Chapter 21

THE SOIL FAUNA OF TROPICAL SAVANNAS. I. THE COMMUNITY STRUCTURE

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INTRODUCTION

The fauna of the soil compartment of terrestrial ecosystems is rich in species and varied in function. Following Bachelier (1971), it can be considered that the two major characteristics which determine the place of a given soil animal within an edaphic community are its adult body size and its mode of respiration. Indeed, both of these characteristics emphasize the ways in which the organism is adapted to the two major features of the soil environment: the very limited space available for living animals within the soil, and the watery nature of this milieu.

Three main life-styles can be observed among soil animals. The smallest are definitely aquatic and spend their whole lifetime within the very small amount of water found in soil pores of various size. Such hydrobionts — soil protozoans, rotifers and nematodes — very seldom reach a body length of 0.2 mm; they constitute the soil microfauna.

The micro-arthropods and enchytraeid earthworms are a little larger in size. Although depending heavily on soil moisture, they have an aerial mode of life, and their size which ranges from 0.2 to 4 mm, enables them to move freely within the soil. They make up the soil mesofauna.

Burrowing animals constitute the soil macrofauna. Their size being larger than that of soil pores, they have to force their way actively through the soil. Some of them do it by using powerful fossorial fore legs; this is the case for mole crickets (Gryllotalpidae) and cicada larvae (Cicadidae). Other animals, such as earthworms, literally eat their way through the soil, whereas ants and termites build elaborate subterranean networks of galleries and nest chambers where they spend most of their lifetime.

The structure of a soil animal community is based upon the trophic relationships of its member species. The staple food source is the litter, made up both of leaves and dead wood on the soil surface, and the roots and soil organic matter within the soil itself. In most tropical savannas, the litter is scarce as it is regularly destroyed by grass fires (see Ch. 4 and Ch. 30); roots consequently represent the major food source for soil animals (Lavelle and Schaefer, 1974). They are eaten live or dead, or as amorphous humic material once decomposed. It is also possible, if not likely, that many consumers of dead organic material also feed actively upon living micro-organisms. Such trophic relationships between animals and micro-organisms within the soil being so far little studied, four major trophic categories of soil animals can provisionally be distinguished: the litter eaters, the root eaters, the soil eaters and the predators.

The structure of the animal communities of savanna soils is also greatly influenced by some environmental factors, even more so than in many other terrestrial ecosystems. Seasonality of climate acts strongly upon soil moisture and soil temperature, thus exerting a strong selective pressure upon soil organisms.

TAXONOMIC STRUCTURE OF SOIL ANIMAL COMMUNITIES IN TROPICAL SAVANNAS

Four study sites have been chosen to illustrate the taxonomic structure of soil animal communities in tropical savannas, as compared with those of the

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tropical rain forest and temperate latitudes. To make this inter-biome comparison even more valid, the sites studied were sampled in the same way, at the same time of the year and by the same observer in three cases out of four (Table 21.1).

The derived (southern Guinean) savanna of Lamto is located in the south of the Ivory Coast. The mean annual rainfall is 1275 mm and the dry season is of a short duration and not rigorous; the soil pF never exceeds 4.2 for more than a month, on the average (Athias et al., 1975). The Laguna Verde pastures, in the State of Vera Cruz, Mexico, were created a century ago at the expense of a mature rain forest. The mean annual rainfall reaches 1500 mm and some forest relicts allow a comparison with the parent soil animal community (Lavelle et al., 1981).

The Foro Foro northern Guinean savanna is located about 250 km north of Lamto in the Ivory Coast. Although the annual rainfall averages 1150 mm, the climate is harsher than in the southern Guinean savanna and the soil remains at a pF of over 4.2 for at least two months every year (Lavelle, unpubl. results). The temperate grassland of Spiboke, shown here by comparison, is located in the south of Sweden; the mean annual rainfall is 520 mm and the average yearly soil temperature is 4.8°C (Persson and Lohm, 1977).

The microfauna of tropical savanna soils has seldom been studied, and quantitative studies are

TABLE 21.1

Numbers (N; ind. m^{-2}) and biomasses (B; g m^{-2}) of various soil animal groups in various tropical and temperate sites

Taxa	Lamto[1] (Ivory Coast)		Foro Foro[2] (Ivory Coast)		Laguna Verde[2] (Mexico)				Spiboke[1] (Sweden)	
	southern Guinean savannas		northern Guinean savannas		pastures		tropical forest		temperate grassland	
	N	B	N	B	N	B	N	B	N	B
MICROFAUNA										
Protozoa	32 × 10⁶	0.21								
Nematoda	1.1 × 10⁶	0.35								
MESOFAUNA										
Enchytreidae	700	0.30							23 800	3.40
Acari	17 500	0.18			25 000		49 300		112 000	0.52
Collembola	1 800	0.045			4400		7000		109 000	0.56
Other micro-arthropods	5100	0.47			3200		2400		1100	0.08
Total micro-arthropods	25 100	1.00			32 600		58 700		222 100	1.16
MACROFAUNA										
Earthworms	230	49.0	460	22.3	700	47.0	132	9.80	133	23.72
Chilopoda	7	0.037	44	0.22	14	0.10	106	0.76	0	0
Diplopoda	43	0.326	59	0.51	19	0.60	311	12.54	2	0.12
Arachnida	4	0.025	3.2	0.10	74	0.90	129	1.40	197	0.16
Coleoptera	230	0.285	28	1.30	320	45.0	122	2.40	1420	11.60
Diptera	16	0.028	0.5	0.05	60	0.10	79	0.60	5600	2.61
Hymenoptera	500	2.00	1400	2.10	570	1.09	1400	1.62	109	0.096
Isoptera	910	1.95	1200	2.80	2		500	1.07	0	0
Others	75	0.094	12	0.30	71	1.20	232	3.39	103	0.28
Total macrofauna	2015	53.75	3207	29.68	1830	96.00	3011	33.58	7564	38.59

[1]Annual average. [2]Wet season.

particularly scarce. The density of soil protozoans reaches 32×10^6 ind. m^{-2} at Lamto (Couteaux, 1976, 1978; Buitkamp, 1971); this is a low density, as compared with the figures published for some temperate sites, which range from 100 to 500×10^6 ind. m^{-2} (Bachelier, 1971). The situation is the same for soil nematodes. Their density in Lamto has been estimated at 1.1×10^6 ind. m^{-2} at Lamto (Malcevschi, 1978) and from 3 to 8×10^6 ind. m^{-2} in various moist Uganda savannas (Banage and Visser, 1967); in temperate grasslands the nematode density averages 10×10^6 ind. m^{-2} (Bachelier, 1971).

The mesofauna of tropical savanna soils is better known, and the results reached by the various investigators are generally in accordance. The enchytraeid earthworms, very numerous in cold and acid soils, are very scarce here; their density never exceeds 1000 ind. m^{-2}, whereas it averages 23 800 ind. m^{-2} at Spiboke, Sweden, and reaches 100 000 ind. m^{-2} in the arctic tundra and 750 000 ind. m^{-2} in the boreal forest (Swift et al., 1979). The average density of micro-arthropods is of the order of 20 000 to 30 000 ind. m^{-2} (Salt, 1952, 1955; Covarrubias et al., 1964; Ryke and Loots, 1967; Belfield, 1971; Athias, 1974; Lavelle et al., 1981). Acari are the most numerous, whereas Collembola are far less abundant. Micro-arthropods are more numerous in tropical rain-forest soils; in the Laguna Verde (Mexico) relict forest patches they reach 58 700 ind. m^{-2}, and 72 700 ind. m^{-2} in an Amazonian forest (Beck, 1971). In Sweden, densities can reach 222 100 ind. m^{-2} at Spiboke.

Four taxonomic groups are dominant over the others in the macrofauna: earthworms, termites, ants and beetles, the latter being mostly represented by larvae.

In the tropical savannas and grasslands studied to date, the earthworm communities reach densities ranging from 234 to 700 ind. m^{-2}, with biomasses varying from 22.3 to 49.0 g fresh weight m^{-2}. Such values clearly exceed those found in nearby rain-forest areas (for instance 9.8 g m^{-2} in Laguna Verde relict forest patches, and 3.5 g m^{-2} in the Lamto gallery forests); they are of the same order of magnitude as the Spiboke biomass (23.7 g m^{-2}), but much lower than those of warmer temperate regions in Europe, where figures ranging from 56 to 287 g fresh weight m^{-2} have been reported (Edwards and Lofty, 1972). Earthworms are therefore the dominant taxonomic group in many tropical savanna soils.

The numbers of ants and termites found in savannas are very high, but their biomass is small, due to their diminutive size. At best, they reach a few grams per square metre; but the specific roles of these insects and their omnipresent activities make them very important components of the soil animal community. Furthermore, these arthropods are less dependent on environmental conditions than earthworms; therefore, their relative importance increases in the drier savannas where the earthworm community is far less numerous (see Ch. 22).

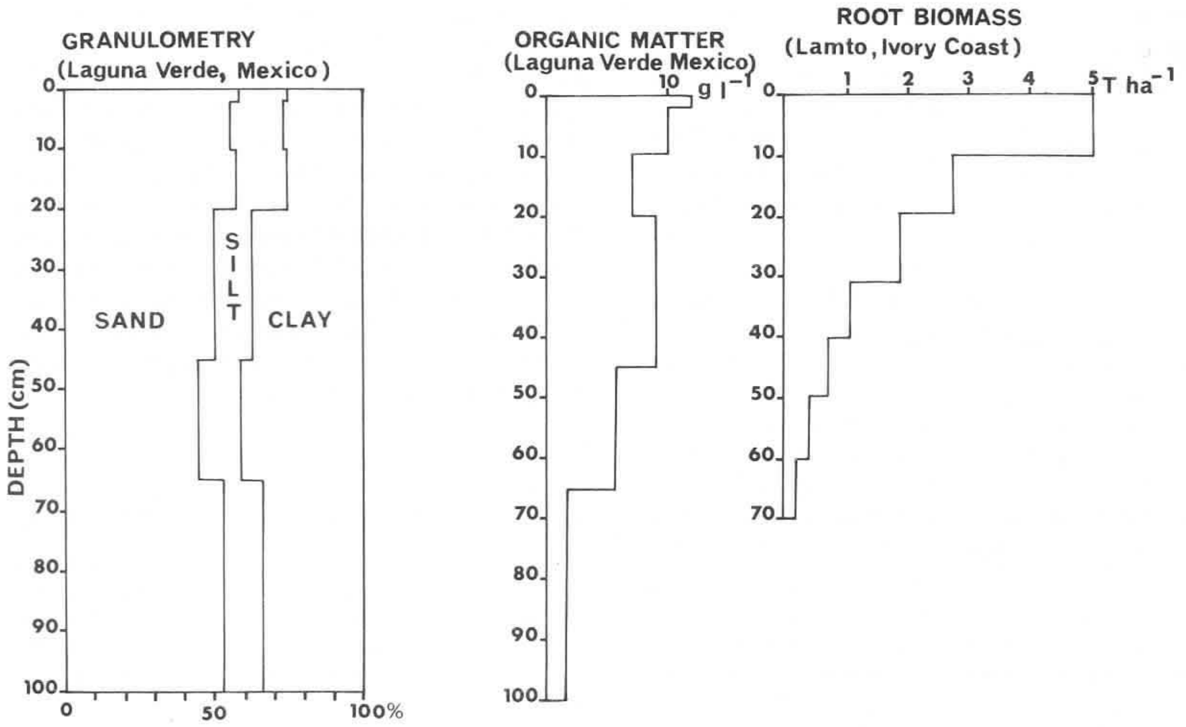
Termites are very numerous in many tropical grasslands, and their functions within the soil compartment of the savanna ecosystem are very diverse (see Ch. 23); however, their role in Laguna Verde grasslands was very limited as their populations were small. This might be a general feature of Neotropical grasslands, but needs to be supported by more data. The density of ants does not vary much between the various savanna categories, although it increases in shrub savannas where resources are more varied than in open grasslands (see Ch. 24).

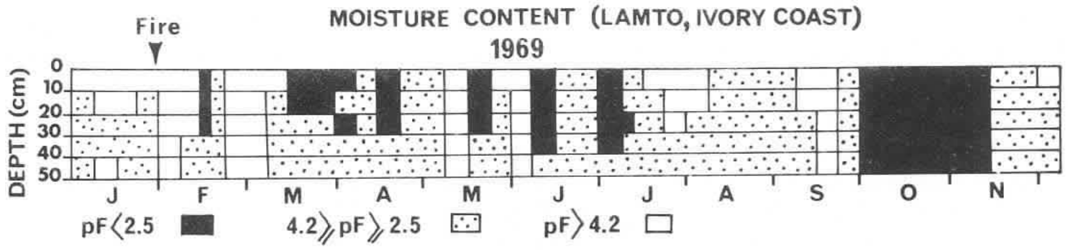
Beetles are of secondary importance, as compared to termites and ants. In some situations, however, they can reach a sizable biomass. Such was the case in Laguna Verde grasslands, where the biomass of beetle larvae was of the same order of magnitude as that of earthworms. Myriapoda are not numerous in savanna soils, being more abundant in forest environments.

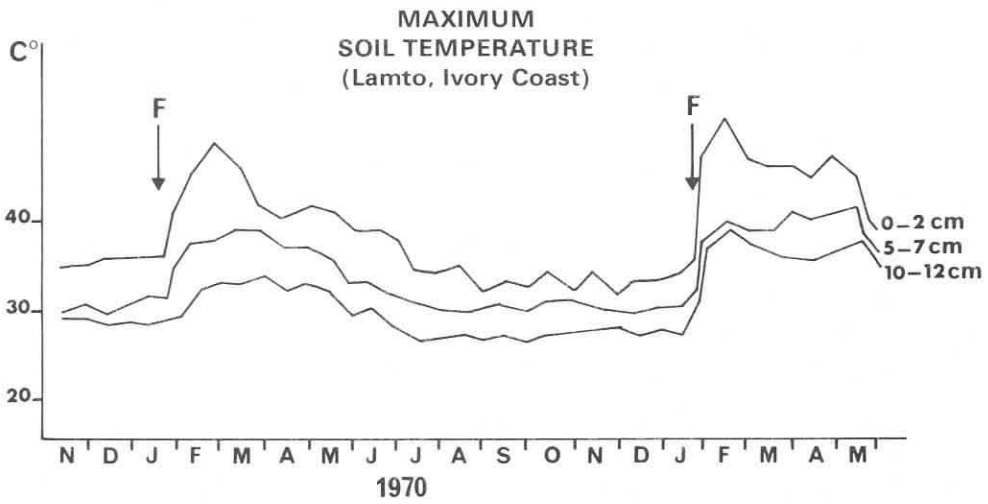
On the whole, the densities and biomasses of animal communities of the tropical savanna soils are lower than those of temperate grasslands, but greater (at least in biomass) than those of tropical rain forests. However, this relative poverty is more apparent than real. In tropical latitudes the high metabolic rate of soil invertebrates is much greater than that of a similar biomass of related species in temperate conditions, due to the high soil temperatures prevailing throughout the year.

DISTRIBUTION IN SPACE

One of the fundamental characteristics of the soil environment is its disposition in more or less distinct horizontal layers, termed soil horizons,


GRANULOMETRY
(Laguna Verde, Mexico)
SAND
SILT
CLAY
DEPTH (cm)
0
50
100%
ORGANIC MATTER
(Laguna Verde Mexico)
10 g l^{-1}
ROOT BIOMASS
(Lamto, Ivory Coast)
1 2 3 4 5 T ha^{-1}


MOISTURE CONTENT (LAMTO, IVORY COAST)
1969
Fire
DEPTH (cm)
J F M A M J J A S O N
pF⟨2.5
4.2≫pF≫2.5
pF⟩4.2


MAXIMUM
SOIL TEMPERATURE
(Lamto, Ivory Coast)
C°
F
F
0–2 cm
5–7 cm
10–12 cm
N D J F M A M J J A S O N D J F M A M
1970

which differ in their physical, chemical and biological characteristics (Fig. 21.1). This also applies to savanna soils, and it is possible to identify species peculiar to the litter and others that are found mostly in deeper soil horizons (Table 21.2). The vertical layering of soil animals is the end result of the vertical gradients in temperature, organic matter content, texture and moisture existing within the soil.

Besides this vertical stratification, the distribution of soil animals in an horizontal plane is also influenced by the plant cover in savanna communities. For example, the soil arthropods are always more numerous under grass tussocks than under the bare areas that are found between clumps of grass (Athias, 1974; Malcevschi, 1978). This is shown in Table 21.3 for the Lamto savanna. The microrelief also plays a role; some earthworm populations apparently congregate under areas where rain water flows out most frequently (Fig. 21.2) (Lavelle, 1978). The presence of trees also influences the distribution of soil animals. The end result of all these factors is an horizontal mosaic of areas characterized by their microrelief and vegetation, each being in turn subject to vertical gradients of food availability and microclimatic

TABLE 21.2

Vertical distribution of various animal taxa in Laguna Verde (Mexico) pastures, and in near-by forest patches; the figures given are the percentages of the total population sample found in different soil layers

Taxa	Pastures				Taxa	Forest patches				
Depth (cm):	0–10	10–20	20–30	30–40		litter	0–10	10–20	20–30	30–40
Glossoscolecidae	91.9	6.8	1.2		Blattaria	63.3	13.3	23.3		
Carabidae (larvae)	91.6	8.4			Araneae	62.9	26.3	5.9	3.2	
Isopoda	90.9	9.1			Isopoda	54.6	34.3	11.1		
Elateridae (larvae)	88.2	7.9	1.3	2.6	Hemiptera	41.4	44.8	1.4		
Blattaria	86.2	13.8			Formicidae	29.2	54.9	15.9	9.5	7.4
Hemiptera	84.1	13.6	0.3		Iulidae	28.7	58.7	7.6	4.9	
Melolonthinae (larvae)	83.3	12.8	3.7		Chilopoda	21.9	54.4	18.5	4.2	1.0
Diptera (larvae)	83.0	13.2	3.8		Diptera (larvae)	18.5	43.1	30.8	7.7	
Araneae	82.2	11.1	6.8		Coleoptera (adults)	16.2	37.8	27.0	6.8	
Megascolecidae	81.3	11.4	3.2	0.2	Symphyla	9.0	74.6	14.9	1.5	
Coleoptera (adults)	76.2	17.8	1.5	4.4	Elateridae (larvae)	7.5	71.2	18.2	3.0	
Formicidae	72.0	15.3	9.4	3.3	Mermithidae	4.7	9.4	32.9	52.9	
Eumolpinae (larvae)	30.0	19.1	35.5	15.5	Chrysomelidae (larvae)	4.0	50.0	21.0	14.0	3.3
Mermithidae	25.7	31.3	37.4	8.7	Polydesmida	3.7	90.0	4.2	2.1	
Symphyla	17.5	60.8	14.8		Oligochaeta	0.1	70.2	22.4	6.2	
					Melolonthinae (larvae)		53.3	30.8	15.0	0.8

TABLE 21.3

The influence of the rhizosphere on the density of soil nematodes and soil micro-arthropods in the Lamto savannas (after Athias, 1974; and Malcevschi, 1978)

	Nematodes (ind. kg^{-1} of dry earth)	Micro-arthropods (ind. m^{-2}, yearly average)
Near the rhizosphere	8975 ± 1890	16 600
Far from the rhizosphere	2395 ± 135	36 900

Fig. 21.1. Variations with depth of some microclimatic and trophic soil parameters (after César and Menaut, 1974; Lavelle, 1978; Lavelle et al., 1981).

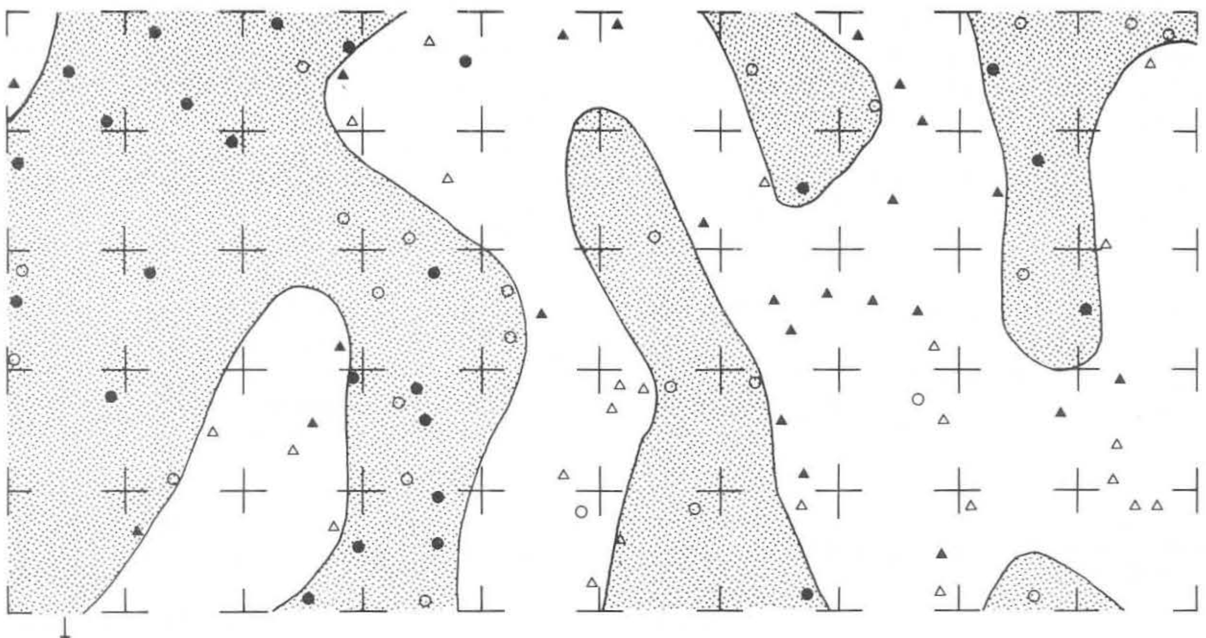


Fig. 21.2. Horizontal distribution pattern of eudrilid earthworm populations in a grass savanna at Lamto, Ivory Coast. Classification of the twelve monthly samples according to their density: ● = 1–3 months; ○ = 4–6 months; △ = 7–9 months; ▲ = 10–12 months. Dotted areas indicate zones of high concentration of worms (Lavelle, 1978). Scale: 15 mm = 10 m.

conditions. Such a pattern of distribution of soil animals is not at all restricted to savanna ecosystems, but it is quite probably more pronounced here than elsewhere, because of the marked seasonal variations in temperature and moisture gradients, as well as the clumped distribution of grass roots in the top soil.

THE TROPHIC STRUCTURE OF SOIL ANIMAL COMMUNITIES IN TROPICAL SAVANNAS

It is still far too early to attempt a description of the food web of the animal community in the soil of tropical savannas. Too little is known concerning the diet and feeding habits of the hundreds of participating species, mostly among the arthropods. All that can be done at present is to divide up the major taxonomic categories into a few broad trophic groups, in order to understand the ways in which the available resources are allocated (Table 21.4).

The soil eaters, mostly represented by earthworms and some humivorous termites, appear to be the most important group; these soil animals always represent more than 50% of the soil animal biomass. Root eaters, very scarce in the Lamto savanna (0.3% of the biomass), amount up to 40.3% in Laguna Verde grasslands; this is due to the abundance, possibly seasonal, of beetle larvae in this study site. Detritivores, mostly litter eaters, represent 17.6% of the soil animal biomass in annually burnt savannas at Lamto. This percentage increases with the importance of bush encroachment. After ten years of fire protection in Lamto it reaches 38.5%. The acompanying increase of predators, from 4.6 to 8.9%, can be explained by the fact that these animals mostly prey upon detritus feeders.

In the rain forest the dominant group is also constituted by the detritus eaters and their predators (65.9% at Laguna Verde), to the detriment of the soil eaters (30.6%) and the root eaters (3.8%).

Inasmuch as the limited number of data can allow one to draw any preliminary conclusion, the soil fauna of tropical savannas can be characterized by a predominance of soil-eating animals, which are always much more numerous than in temperate

TABLE 21.4

Biomass percentages of the four main trophic categories of soil animals at Lamto and Laguna Verde (after Athias et al., 1975; and Lavelle et al., 1981)

	Soil eaters	Root eaters	Detritus eaters	Predators
Lamto, burnt savanna	77.0	0.3	17.6	4.6
unburnt savanna	52.5	0.3	38.5	8.9
Laguna Verde, pastures	54.2	40.3	5.5	
forest patches	30.6	3.8	65.6	

grasslands. The increasing importance of detritus eaters and predators, combined with the progress of bush encroachment, also appears to be a characteristic feature of these communities.

ENVIRONMENTAL FACTORS INFLUENCING THE STRUCTURE OF ANIMAL COMMUNITIES IN SAVANNA SOILS

The soil environment is actually much more complex than it commonly appears. Climatic, edaphic and biotic parameters interact continuously, not to mention the interference of man. Only a multivariate analysis of the data collected at different times of the year on a single site, together with the comparison of different facies of a single savanna type, can help to identify the roles played by the various environmental factors.

Such an analysis has been carried out in the Lamto savanna by Lavelle and Meyer (1980). Eight factors have been identified which are responsible for 63.7% of the total variance for the thirteen variables studied. Most of these factors can be linked to environmental variables such as grass fires, soil moisture, soil temperature, microclimatic consequences of an increase in shrub cover and physical structure of the soil.

As discussed in Chapter 30, the effect of grass fires is manifold. The rise in temperature of the upper parts of the soil profile during the passage of the burning front not only immediately kills a number of organisms, but decreases soil moisture so that the pF rises above 4.2, a value which is lethal for many hygrophilous species. However, the most important consequence of grass fires for soil animals is the destruction of the litter which results in a drastic reduction of food resources for the soil animals. Repeated destruction of the litter in tropical savannas probably explains the predominance of soil eaters in this kind of environment, the only abundant and continuously available food sources being the roots and the soil organic matter.

The water regime of the soil obviously depends on the yearly amount of rainfall and its seasonal pattern of distribution; but it is also determined by the water-holding capacity of the soil, the local topography and the nature of the vegetation cover. As shown in Chapter 22, earthworms are most sensitive to changes in soil moisture, but this is also true of some other taxonomic groups such as the Collembola and Myriapoda. Conversely, the soil mites (Acari) apparently favour drier conditions (Athias, 1974; Athias et al., 1975) and social insects are little affected by this factor.

Changes in soil temperature have multivarious consequences. They influence the circadian rhythms of activity of many species (Lavelle, 1971; Lévieux, 1971) and the overall activity level of some populations (Lavelle, 1978), as well as their vertical movement within the soil (Belfield, 1971; Athias, 1974).

The nature of the plant cover is also important, as it affects both the microclimatic conditions of the soil below the vegetation layer, and the amount of food made available to soil organisms in the litter. Whereas the shade afforded by vegetation tends to reduce water loss at the soil level, it must be remembered that the evapotranspiration of shrubs exceeds that of grasses. This leads to a decrease in the water content of the soil at depths ranging from 20 to 40 cm, where the density of shrub roots is the highest. At Lamto, for instance, the increase in numbers of litter-eating animals corresponds to a decrease in soil-eating earthworms when shrub cover becomes more important in fire-protected savannas.

The chemical and physical structure of the soil is

also of great importance for soil animals. The amount of organic matter available in tropical savannas is always small; it does not exceed 1 or 2% in the topsoil, but its local variations can influence the local distribution of soil animals (Lavelle et al., 1979). The granulometric composition of the soil is often even more important, as it influences its water-holding capacity and its porosity — hence the ability of animals to penetrate into it.

The depth of the soil is also an important factor for soil animals which have to move in deeper horizons during the dry season. In some instances the shallowness of the soil, or the presence of a hard gravelly horizon, can be important limiting conditions for soil organisms.

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